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PAPERS.

24. The Head Cavities and Development of the Eye Muscles in *Trichosurus vulpecula*, with Notes on some other Marsupials. By ELIZABETH A. FRASER, B.Sc. (Lond.), F.Z.S., Embryological Laboratory, Department of Zoology, University of London, University College.

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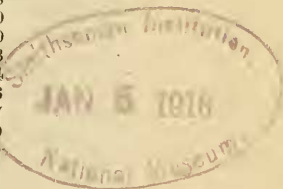
(Plates I., II.* and Text-figures 1-26.)

INDEX.	Page
Introduction	299
Material	302
The Eye Muscles of the Adult	303
Description of Material	304
Summary of Events in <i>Trichosurus vulpecula</i>	328
Notes on other Marsupials	330
<i>Phascogale</i>	330
<i>Phascogale</i>	333
<i>Macropus</i>	334
<i>Perameles</i>	336
<i>Didelphys</i>	337
<i>Dasyurus</i>	339
Concluding Remarks	339
Bibliography	342

INTRODUCTION.

The following investigation of the head-cavities and development of the eye muscles of *Trichosurus vulpecula* was undertaken at the suggestion of Professor J. P. Hill, whose help and advice I gratefully acknowledge. All the material examined was

* For explanation of the Plates see p. 346.



obtained from Professor Hill's excellent collection of young stages of marsupials.

Cavities in the mesoderm of the anterior (preotic) region of the head, bounded by more or less definite epithelial walls, have been described in many vertebrates, and they are now considered by the majority of observers to represent somites comparable with those of the trunk. They were first observed in Selachians by Balfour ('78), later by Milnes Marshall ('81), van Wijhe ('83), Dohrn ('90) ('04), and since then by many other investigators in different fishes.

In Amphibians, cavities have been seen by Scott and Osborne ('79) in the newt and in the Gymnophionan *Hypogeophis* by Marcus ('09). They appear to be absent in *Necturus* (Julia Platt, '94); in the frog (Corning, '99) and in the toad (Edgeworth, '99) the anterior somites in the head are apparently solid, although Goette ('75), in his classical work on the development of the toad, appears to refer to them as cavities.

Van Wijhe ('86) was the first to point out the occurrence of head-cavities in birds and reptiles. In birds, Rex has more recently studied them in the duck ('97) and in the gull ('01) ('05), Edgeworth ('07) in the fowl, and Professor Hill has directed my attention to the occurrence of large premandibular cavities in sections of early emu chicks in his collection.

The conditions in reptiles concern us more closely and may be considered in greater detail. In this class three somites have been observed in the preotic region of the head, of which the first or premandibular develops into a large and conspicuous cavity surrounded by epithelial walls, the cavities of either side at some time of their development being usually connected across the middle line by a transverse canal as in fishes. The second and third somites are small and more difficult to determine, and observers differ considerably in their accounts of them. Van Wijhe ('86) did not discover a second somite in *Lacerta* and he describes the third somite as solid; Hoffmann ('90), on the other hand, finds three hollow somites behind the premandibular, but whether the last two both belong to the third head somite or whether they correspond to somites three and four of fishes, he was unable definitely to decide. Again in *Lacerta*, Corning ('99) recognises the third somite but no similar second somite, the m. obliquus superior, which usually develops from the latter, here being described as arising from the dorsal part of the primordium of the trigeminal musculature which grows out over the eye. In *Anguis fragilis*, both the second and third somites were seen by Oppel ('90), each of which contained a small central cavity, but the second was much less distinct than the third. In the Chelonians the same somites are present, but whereas in *Emys lutaria*, according to Filatoff ('07), the third is solid, in *Chelydra serpentina*, described by Johnson ('13), both second and third possess a distinct cavity round which the cells are arranged in a radial manner.

The occurrence of large anterior head-cavities followed by corresponding structures behind them, has led to much discussion on the metamerism of the vertebrate head. As one advances in the scale of vertebrates, however, the segmentation in the mesoderm of the preotic region of the head becomes more and more obscure, until in the Mammalia only traces remain of a former metameric condition. No definite head-cavities have ever been observed in mammals, although probable remnants of these have been found in man by Zimmermann ('98). In the rabbit, although the first head somite arises much as in reptiles from the fore-end of the alimentary canal as a solid outgrowth (Corning '99), or as a hollow one soon becoming solid (Edgeworth '11), it never acquires a cavity as in lower vertebrates but in later stages forms a small solid mass of cells behind the optic cup on each side, difficult to distinguish from the surrounding tissue. Reuter ('97), who has studied the pig, sees there no signs of primitive segments in the head and considers the eye muscles as a completely independent formation arising from an accumulation of mesenchyme cells; his observations, however, begin at a late stage and no early embryos are described.

It was first noted by Milnes Marshall ('81) in Elasmobranchs and is now well established, that the walls of the premandibular cavity give rise to four muscles of the eye, the mm. recti superior, inferior and internus and the m. obliquus inferior, all innervated by the oculomotor nerve; that the second head somite contributes the m. obliquus superior supplied by the trochlear nerve, while the third furnishes the m. rectus externus and, in reptiles and mammals, the m. retractor bulbi, both these muscles being supplied by the abducens nerve. We have an exception to the usual conditions in *Petromyzon*, where the innervation of the muscles is peculiar. According to Fürbringer ('75, p. 70), "Die Innervation der Augenmuskeln anlangend besteht bei den Petromyzonten die Eigenthümlichkeit, dass, während der Oculomotorius der Fische sämtliche Augenmuskeln mit Ausschluss des Rect. ext. und Obliq. sup. versorgt, hier der Rect. inf. nicht vom Oculomotorius, sondern vom Abducens innervirt wird, so dass also der Abducens 2 Augenmuskeln versorgt. Dieses Verhalten ist vielleicht dahin zu deuten, dass der Rect. int. den vereinigten Rect. int. und Rect. inf. entspricht und dass in gleichem Masse, wie diese beiden Muskeln sich späterhin in 2 gesondert, der Rect. inf. mit dem Rect. ext. verschmolzen, einen einzigen durch den Abducens innervirten Muskel vorstellend."

The conditions in Amphibia also do not seem to coincide with those in other groups and the views of different authors are very conflicting. Marcus ('10) has studied the Gymnophiona in some detail, and according to his account of *Hypogeophis* the mandibular somite, at first connected by a transverse bridge with its fellow of the opposite side, develops into a large cavity surrounded by a single layer of epithelial cells lying postero-dorsally to the eye, and from which a cell-strand grows down into the mandibular

arch (see his fig. V, p. 139, Marcus, '09). The premandibular cavity, which is small and has also in early stages a connecting median portion, partly degenerates, but a small part moves up to the mandibular cavity and completely unites with the rostral side of the latter. All the eye muscles, except the m. rectus externus derived from the third somite, take their origin from the mandibular cavity which is innervated by the oculomotor and perhaps also by the trochlear nerve. Marcus ('10) further states (p. 409):—"Daher glaube ich, das, wenn auch Prämandibularzellen sich mit der Mandibularmasse vereinigt haben, nicht deswegen der Oculomotorius die Mandibularhöhle innerviert, sondern dass er ganz primär der zugehörige Nerv ist. Dies ergiebt sich, ausser durch die naive Betrachtung, auch durch folgende Ueberlegung. Aus dem rostralsten Teil der Mandibularhöhle entwickelt sich der Musc. obliquus superior, also ein vom Trochlearis innervierter Muskel. Die Zellmasse, woraus er sich entwickelt, glaube ich aus der Prämandibularmasse ableiten zu können. Exakt beweisen kann ich diese Behauptung freilich nicht, weil bei der Muskelbildung die Mandibularhöhle schon mesenchymatös war, also die Muskelbildung nicht so scharf wie bei Selachiern verfolgt werden kann; aber aus der Topographie der Gebilde ergibt es sich, das zur Bildung des Musc. obliquus superior wie bei Selachiern so auch bei *Hypogeophis* dieser Abschnitt der Mandibularhöhle verwendet wird."

Although many authors have given accounts of the origin of these preotic somites and of the first development of the eye muscles from their walls, few have traced in detail the further growth of these muscles until their adult position is reached. In reptiles and mammals this latter growth is more difficult to follow owing to the development of the m. retractor bulbi. The most complete account in reptiles is that of *Chelydra serpentina* by C. E. Johnson ('13), and the only description in mammals is that of Reuter's paper ('97) on the pig, above mentioned. The following observations on the marsupial *Trichosurus vulpecula* will therefore be of some interest.

MATERIAL.

The material examined comprises twelve stages of *Trichosurus vulpecula*, eight embryos and four pouch young of *Phascolarctos cinereus*, five embryos of *Phascolomys mitchelli*, an embryo and a fœtus of *Macropus*, five embryos and one pouch young of *Perameles*, one embryo of *Didelphys* and a good series of *Dasyurus*.

Two wax-plate models of the optic cup and primordia of the eye muscles were made and are reproduced on Plates I. & II. I am much indebted to Miss E. A. Steele for her excellent coloured drawings of these models. The terminology of the arteries and veins in the head has been adopted from Grosser's account of the development of the vascular system in the Chiroptera ('01) and

also from the description of the development of the veins of the head in reptiles by Grosser and Brezina ('95).

THE EYE MUSCLES OF THE ADULT.

Adult specimens of *Trichosurus* and *Dasyurus* were examined, and the usual eye muscles, including a well-developed m. retractor bulbi, were found to be present. In 1902, Corning ('02) described in some detail the eye muscles of the cat, and his account is generally applicable to the recti and oblique muscles of the marsupial. The only noteworthy difference is in regard to the form of the m. rectus externus which in marsupials has a double origin, the two portions uniting to have a common insertion on the eyeball.

The m. retractor bulbi shows considerable variation in different mammals. When present, it always arises further caudally than the m. rectus externus but enters the orbit together with the mm. recti and the m. obliquus superior, and its insertion in the bulbus lies nearer the optic nerve than the other muscles. According to Motais ('87), who has studied this muscle in many mammals, the m. retractor bulbi attains its maximum development in ruminants; he also observed its relatively large size in the opossum. He further states, p. 56: "Le muscle choanoïde peut offrir un ou plusieurs interstices cellulieux qui le divisent en deux ou plusieurs parties. Ces interstices sont larges dans les carnivores et séparent le muscle en quatre faisceaux bien distincts. Ordinairement, les lignes de séparation sont moins nettes; dans les solipèdes et les ruminants, les bords des deux divisions du muscle s'envoient réciproquement des fascicules . . . Dans le porc, on ne trouve qu'un seul interstice assez large au milieu du muscle droit inférieur." Similar conditions to those in the pig are found in rodents; the same author, in his description of the rabbit, p. 206, says: "Il [le muscle choanoïde] forme un cône régulier qui n'est interrompu que par un seul interstice cellulieux situé au-dessous du muscle droit supérieur. Cet interstice se prolonge jusqu'à l'insertion bulbaire du nerf optique et le long du nerf lui-même, jusqu'au trou optique." In the cetaceans (Weber, '86) the same variations occur; here again, the muscle may be present as an almost complete circular sheet surrounding the optic nerve or it may be divided into four parts, each more or less united by connective tissue.

In *Trichosurus* and *Dasyurus*, as in other mammals, the m. retractor bulbi has a more deeply seated origin than the other muscles. It arises from the basisphenoid and passes forwards to enter the orbit between the two portions of the m. rectus externus. Surrounding the optic nerve, it extends outwards as a muscular sheet which gradually increases in circumference up to its insertion round the inner side of the eyeball within the recti muscles. Although appearing as a completely closed cone, the two edges of the sheet are not fused along the anterior side of the nerve just behind the m. rectus internus.

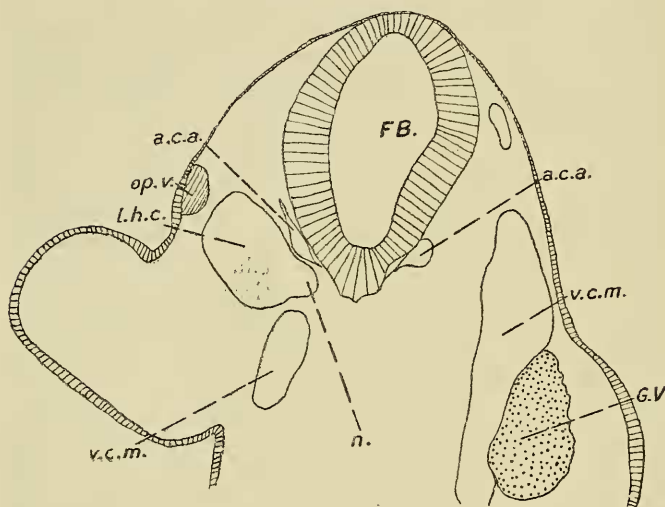
DESCRIPTION OF MATERIAL.

Trichosurus vulpecula. Embryo of G.L. 5 mm. (= Stage I. *a*, *b* & *c*)*. (Text-figs. 1, 2.)

This stage is represented by three embryos, *a* (δ '97), *b* (I.A. '01), and *c* (I. '01), of which (*a*) and (*c*) are cut horizontally and (*b*) longitudinally.

The cavity of the optic vesicle is flattened by the thickening and partial invagination of its lateral wall, and it is connected with the brain by a hollow stalk. The ectoderm opposite the vesicle is thickened.

Text-figure 1.



Trichosurus vulpecula, G.L. 5 mm. (δ '97).

Horizontal section through the head (S 3-4-5), somewhat oblique, passing through the premandibular head-cavity of the left side. $\times 75$ and reduced by $\frac{1}{3}$.

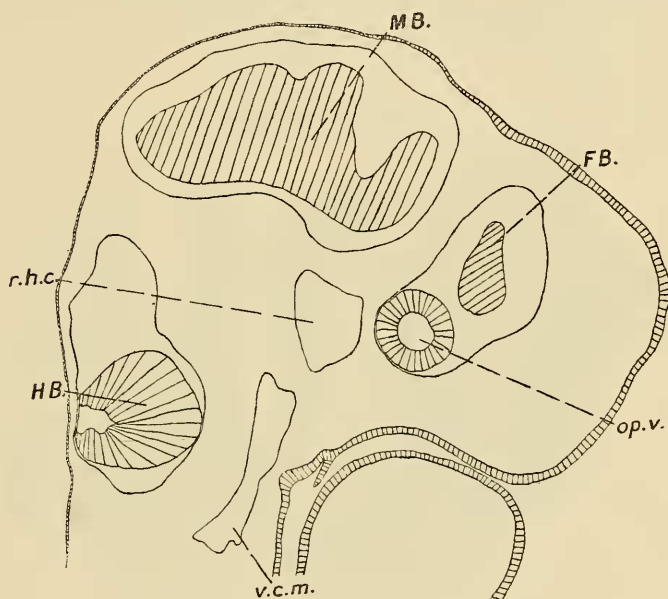
a.c.a.=arteria cerebri anterior, *FB.*=fore-brain, *G.V.*=trigeminal ganglion.
l.h.c.=left head-cavity. *n.*=portion of cavity constricted off from the rest.
op.v.=optic vesicle. *v.c.m.*=vena capitis medialis.

There are two large and conspicuous head-cavities, one on each side immediately posterior to and on the medial side of the optic vesicle, situated ventro-laterally to the fore-brain; between the cavity and the brain runs the anterior cerebral artery. The cavity is lined by a single layer of epithelial cells which is more attenuated on the side farthest from the brain, where it cannot everywhere be distinguished in the sections. The shape of the cavity varies slightly in the three embryos, being obliquely

* *Vide* Fraser and Hill: "The Development of the Thymus, Thyroid and Epithelial Bodies in *Trichosurus vulpecula*," Phil. Trans. Roy. Soc. 1915.

rectangular in cross-section in (*a*) (text-fig. 1, *l.h.c.*), where on the left side it measures .26 mm. in a dorso-ventral direction, .31 mm. antero-posteriorly and .32 mm. transversely; but it is more oval in (*b*), and tapers somewhat towards the eye (text-fig. 2, *r.h.c.*). On both sides in (*a*) a small medial portion is marked off from the main body of the cavity by a constriction, the upper part of which can just be seen in text-fig. 1, *n*. No such condition is present in (*b*) or (*c*), although on the left side of the former there is an incomplete partition across the middle of the cavity; the division in this case, however, may not have the same significance.

Text-figure 2.



Trichosurus vulpecula, G.L. 5 mm. (I.A. '01).

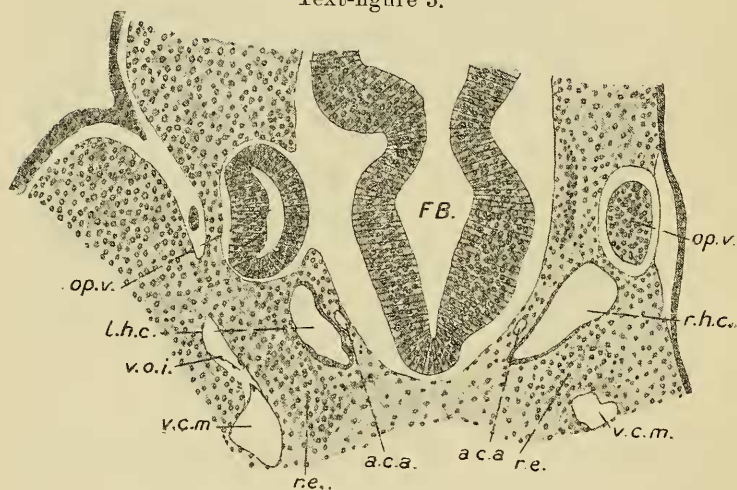
Longitudinal section (S 2-1-13) passing through the premandibular head-cavity of the right side. $\times 75$ and reduced by $\frac{1}{3}$.

FB.=fore-brain. HB.=hind-brain. MB.=mid-brain. op.v.=optic vesicle.
r.h.c.=right head-cavity. v.c.m.=vena capitis medialis.

In embryo (*c*), lying obliquely along the postero-lateral wall of the cavity, on the inner side of the vena capitis medialis, is a slightly more condensed portion of the mesenchyme, representing the third or hyoidean somite and constituting the primordium of the abducens muscle-mass. It runs forwards and laterally just below the origin of the vena cerebialis anterior into another mass of loosely connected cells, which extends downwards round the lateral side of the vena capitis medialis to become united below

with the maxillo-mandibular mesenchyme. On its anterior side this group of looser cells, to which in following stages I have given the name of the intermediate mass and which represents the second or mandibular somite, projects slightly forwards anterior to the cavity; this projection, as we shall see later, is the first indication of the primordium of the *m. obliquus superior*. The intermediate mass is, at the same time, connected with the postero-lateral wall of the cavity for three or four sections. The limits of the complex formed by the intermediate and abducens masses are difficult to determine accurately, as they are not easily distinguished from the surrounding mesenchyme and in embryo (*a*) are still more indefinite. In the longitudinal series, a distinct but small elongated collection of cells stretches along the posterior border of the cavity, apparently representing the abducens mass, but no connection with any maxillo-mandibular mesenchyme is recognisable.

Text-figure 3.



Trichosurus vulpecula. G.L. 4.5 mm. (β '98).

Transverse section (S3-6-13) passing through the premandibular head-cavity on each side. The sections are rather oblique, the cavity of the left side being cut nearer its ventral end. The anterior portion of the abducens muscle-mass lies posterior to the cavity. $\times 110$ and reduced by $\frac{1}{3}$.

a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *l.h.c.*=left head-cavity. *op.v.*=optic vesicle. *r.e.*=anterior portion of abducens muscle-mass. *r.h.c.*=right head-cavity. *v.c.m.*=vena capitis medialis. *v.o.i.*=vena orbitalis inferior.

The Gasserian ganglion is large and the mandibular branch of the trigeminal nerve is already well developed. The oculomotor nerve runs from the mid-brain anteriorly for a short distance but does not reach the head-cavity.

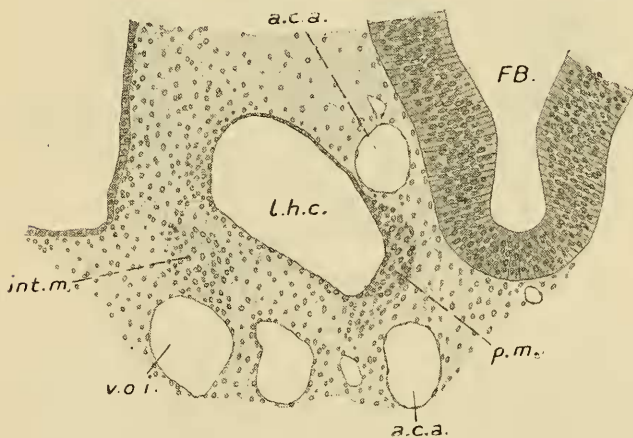
Another embryo (β '98) measuring 4.5 mm. (=Stage II *a*) at its greatest length, may be mentioned here. It is cut transversely and almost at right angles to the last and is slightly older, the optic vesicle being still further invaginated.

The head-cavities are narrow from side to side and have the form in the sections of an elongated triangle, the long pointed end of which runs ventrally and medially (text-fig. 3, *r.h.c.*). They are lined by a single layer of epithelial cells which can be distinguished all round the cavity but which, on the side next the optic vesicle and extending round this side laterally for a short distance, is considerably attenuated. The exact limits of the abducens muscle complex are again very indefinite (text-fig. 3, *r.e.*).

Embryo of G.L. 7 mm. (α '97) (=Stage III.).
(Text-figs. 4-6.)

The cavity of the optic vesicle is very narrow, the outer or retinal layer being much thickened and well invaginated and the adjacent ectoderm now forms a rounded solid inbulging, the primordium of the lens.

Text-figure 4.



Trichosurus vulpecula. G.L. 7 mm. (α '97).

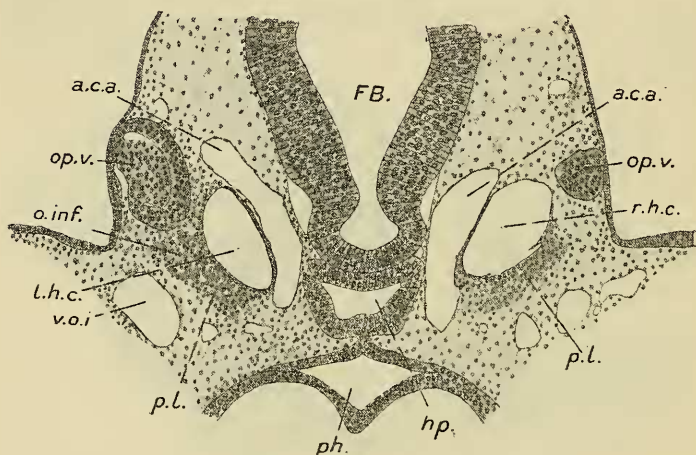
Horizontal section through the head (S 3-2-11), passing above the optic vesicle and through approximately the middle of the head-cavity of the left side (*l.h.c.*), to show the proliferation from postero-medial wall of the cavity (*p.m.*). The ventral end of the intermediate mass is seen postero-laterally to the cavity. $\times 110$ and reduced by $\frac{1}{4}$.

a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *int.m.*=intermediate mass.
v.o.i.=vena orbitalis inferior.

The premandibular head-cavity has only increased slightly in size but changes are to be seen in its walls. About half-way down the cavity on the postero-medial side, the wall has thickened

and is now composed of several layers of cells (text-fig. 4, *p.m.*); immediately ventral to this and on the postero-lateral side occurs a much more extensive proliferation, which extends down as far as the end of the cavity but does not involve the extreme ventral wall (text-fig. 5, *p.l.*). At its lower end, however, a part of this thickening stretches out laterally behind the bulbous and forms the first indication of the m. obliquus inferior (text-fig. 5, *o.inf.*). On the left side, the two proliferations appear to be separate from each other, but on the right the more dorsal one extends round at its lower end to join the larger ventral. Except where proliferation is proceeding the wall of the cavity is very thin; on the side next the brain it consists of a single but perfectly definite epithelial layer, but on the side next the optic cup it is much less definite (text-figs. 4 & 5).

Text-figure 5.

*Trichosurus vulpecula*. G.L. 7 mm. ($\times 97$).

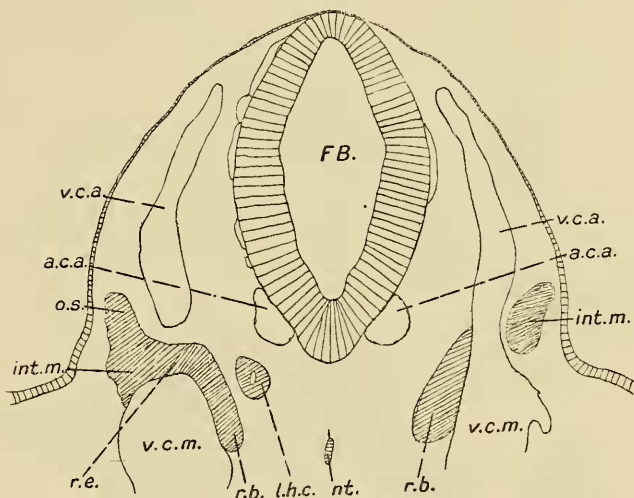
Horizontal section through the head (S 3-3-9), passing through the dorsal portion of the optic vesicle (*op.v.*) and the ventral portion of the head-cavities (*l.h.c.* & *r.h.c.*), to show the proliferation from the postero-lateral wall (*p.l.*). The primordium of m. obliquus inferior (*o.inf.*) is seen on the left side. $\times 75$ and reduced by $\frac{1}{3}$.

a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *hp.*=hypophysis.
ph.=pharynx. *v.o.i.*=vena orbitalis inferior.

The primordium of the abducens muscle-mass consists of a postero-dorsal portion which lies along the medial side of the vena capitis medialis (text-fig. 6, *r.b.*) and which, at its anterior end, runs ventrally outwards to join with the larger anterior portion of the mass (text-fig. 6, *r.e.*). The latter, whose dorsal side surrounds the root of the vena cerebri anterior, lies anterior to the vena capitis medialis and extends half-way down

the head-cavity close to the postero-lateral wall of the latter, its lateral end running into the intermediate mass, the limits of the two being indistinguishable (text-fig. 6, *int.m.*, and also the ventral end in text-fig. 4, *int.m.*). The intermediate mass itself, which is composed of more loosely connected cells, passes on the one hand, forwards into a mass of condensed mesenchyme lying above the optic vesicle on the outer side of the ophthalmic nerve, this portion representing the primordium of the m. obliquus superior (text-fig. 6, *o.s.*); and on the other hand, backwards and

Text-figure 6.

*Trichosurus vulpecula.* G.L. 7 mm. (a '97).

Horizontal section (somewhat diagrammatic) through the head (S 3-1-11), showing the posterior (*r.b.*) and anterior (*r.e.*) portions of the abducens muscle-mass of the left side, which extend in front of the vena capitis medialis (*v.c.m.*), just ventral to the vena cerebri anterior (*v.c.a.*), to unite with the intermediate mass (*int.m.*). The primordium of the m. obliquus superior (*o.s.*) is seen as a forward outgrowth from the intermediate mass. Owing to the obliquity of the sections, the right side is cut at a more dorsal level than the left and only shows the posterior portion (*r.b.*) of the abducens mass lying medial to the vena capitis medialis (*v.c.m.*) and the vena cerebri anterior (*v.c.a.*). $\times 75$ and reduced by $\frac{1}{3}$.

a.c.a.=arteria cerebri anterior. *l.h.c.*=left head-cavity. *nt.*=notochord.

downwards lateral to the vena capitis medialis and is loosely connected with the maxillo-mandibular muscle-mass, the connection here not being well seen. The union of the intermediate mass with the postero-lateral wall of the cavity is most probably again present.

The oculomotor nerve is now thicker and its distal end terminates dorso-laterally to the head-cavity.

From the Gasserian ganglion arise a well-developed mandibular nerve, a small maxillary branch and an ophthalmic nerve.

The abducens is here seen for the first time. It leaves the mid-brain by many fine fibres which unite and run forwards parallel to the side of the brain for a short distance.

Another example of this stage, which measures 7.5 mm. (XIX. '04) (=Stage IV.), presents almost the same features. Although the sections are cut in the same direction, that is horizontally through the head, the head-cavity in section is more triangular and less elongated so that its area is larger than in the 7 mm. embryo above described. The postero-medial and postero-lateral proliferations form one thickening and the vena cerebri anterior appears to be only slightly surrounded by the anterior portion of the abducens muscle-mass.

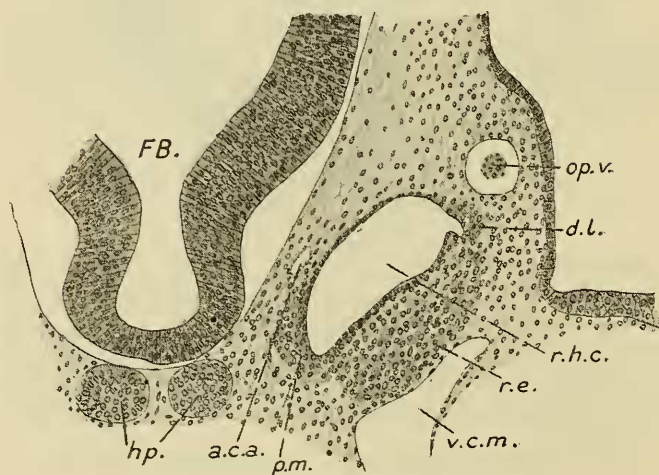
The conditions in this embryo, however, are difficult to make out accurately.

Embryo of G.L. 6 mm. (II. '01) (=Stage V.).

(Text-figs. 7 & 8.)

The cavity of the optic vesicle is still further reduced and the lens is almost separated off from the ectoderm which is closing over it.

Text-figure 7.



Trichosurus vulpecula. G.L. 6 mm. (II. '01).

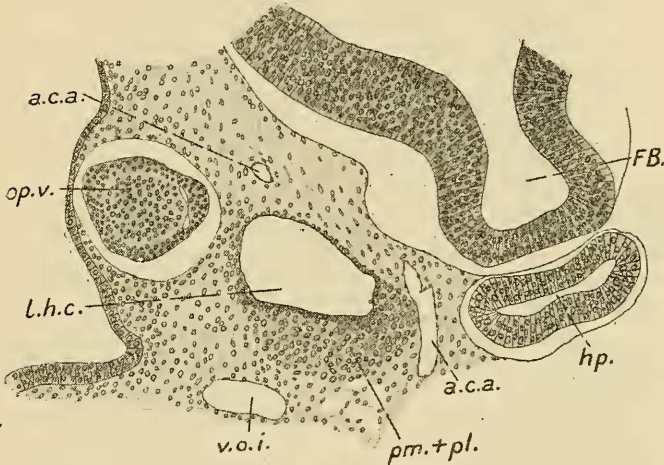
Horizontal section through the head (S 2-4-2), passing just above the middle of the head-cavity of the right side (*r.h.c.*), and showing the proliferating bud on the dorso-lateral wall (*d.l.*) and the thickening on the postero-medial wall (*p.m.*). The anterior portion of the abducens muscle-mass (*r.e.*) lies posterior to the head-cavity and in front of the vena capitis medialis (*v.c.m.*). $\times 116$ and reduced by $\frac{1}{4}$.

a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *hp.*=hypophysis.
op.v.=optic vesicle.

The premandibular head-cavity is large and conspicuous on each side; although at its widest it is only slightly smaller than that of the 7 mm. embryo, the ventral portion is reduced, perhaps owing to further proliferation of the walls.

The proliferation of the postero-medial wall is more extensive; it begins more dorsally and, as the cavity narrows ventrally, it extends round on to the postero-lateral wall, the two thickenings forming one mass (text-fig. 8, *pm.+pl.*). The thickened area is continued on to the extreme ventral wall from which a solid mesodermal mass, the *m. obliquus inferior*, hangs down below the cavity posterior to the optic cup and tapers at its lower end.

Text-figure 8.



Trichosurus vulpecula. G.L. 6 mm. (II. '01).

Horizontal section through the head (S 2-4-8), passing through the dorsal region of the optic vesicle (*op.v.*) and the ventral portion of the left head-cavity (*l.h.c.*), to show the now united postero-medial and postero-lateral proliferations from the wall (*pm.+pl.*). $\times 110$ and reduced by $\frac{1}{4}$.

a.c.a.=arteria cerebri anterior. *fb.*=fore-brain. *hp.*=hypophysis.
v.o.i.=vena orbitalis inferior.

At this stage for the first time, on the dorso-lateral region of the cavity on both sides, the wall shows a distinct, though not very extensive thickening which originates as a bud growing out of the cavity (text-fig. 7, *d.l.*). This bud is the primordium of the *m. rectus superior*.

The cavity is lined by a single layer of cells except where the wall is proliferating.

The abducens muscle complex has increased considerably in size and is more distinct than in our earlier stages. The much larger anterior portion, still connected on its lateral side with

the intermediate mass, lies very close behind the head-cavity and in front of the Gasserian ganglion, being separated from the latter by the vena orbitalis inferior (text-fig. 7, *r.e.*); it extends down along the upper two-thirds of the cavity to the region where the postero-lateral proliferation begins. The smaller postero-dorsal portion runs back as before on the medial side of the vena capitis medialis.

The primordium of *m. obliquus superior* has now grown further forwards from the intermediate mass and reaches anteriorly beyond the distal end of the ophthalmic branch of the trigeminal nerve, on the outer side of which it lies. The connection of the intermediate mass with the maxillo-mandibular mesenchyme is most probably present but could not definitely be made out in this embryo; the mass is again joined with the dorso-lateral corner of the cavity for about three sections.

The oculomotor nerve is stronger and, running down ventrally on the medial side of the vena capitis medialis, now reaches the head-cavity and appears as a small nerve between the wall of the latter and the anterior portion of the abducens muscle-mass; its distal end soon disappears and can only be followed for a short distance alongside the cavity.

The abducens nerve is now well developed and runs forwards on the inner side of the Gasserian ganglion, but it is not very much longer than at the last stage.

Embryo of G.L. 7.75 mm. (XX. '04) (=Stage VI.).

As regards the development of the eye and the muscle-masses this stage is very similar to the last, and only a few observations need be made upon it.

The optic vesicle is not so flattened as at 6 mm. and the lens is still joined with the ectoderm.

The premandibular head-cavity is smaller and pear-shaped, its wider side lying next the eye, and the posterior proliferations are more extensive though the thickening on the ventral wall does not appear to be so marked. No dorso-lateral proliferation was recognised.

The abducens nerve now runs into the pointed posterior end of the dorsal portion of the abducens muscle-mass.

Embryo of G.L. 7.25 mm. (=Stages VII. & VIII. *a* & *b*). (Text-figs. 9-13.)

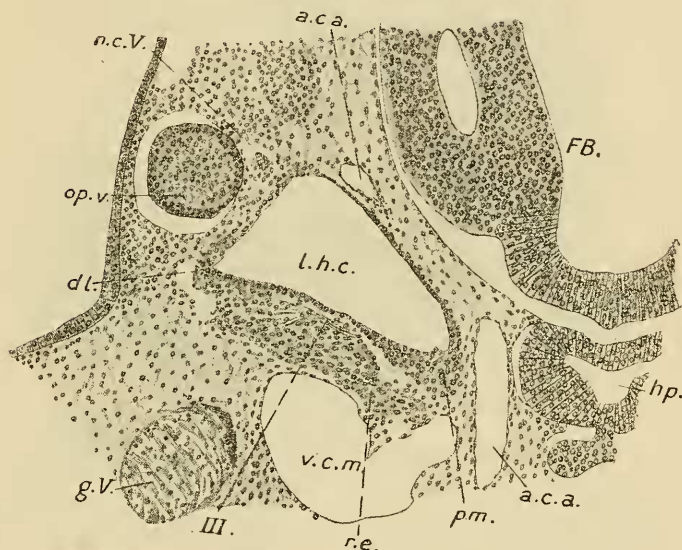
In this next stage there are three embryos, *a* (III. '01), *b* (XII A. '02) and *c* (XII. '02), each measuring 7.25 mm. at its greatest length. Although in many particulars (*a*) is the youngest of the three and (*c*) is slightly older than (*b*), in respect of the eye-muscle primordia very little difference exists between them.

The invagination of the optic vesicle has advanced still further, the cavity being reduced to a narrow slit, but the optic stalk still contains a wide lumen. The lens is closed off from the ectoderm

and forms a hollow vesicle with thickened walls and a central cavity.

In (a) the premandibular head-cavity has attained its maximum size and, at its widest, has roughly the form in horizontal section of a right-angled triangle (text-fig. 9, *l.h.c.*) measuring $\cdot 48$ mm. transversely $\times \cdot 37$ mm. antero-posteriorly $\times \cdot 23$ mm. dorso-ventrally. In (b) and (c) the cavity is smaller than in (a), but is still large, the difference being due mainly to a reduction in the antero-posterior width, which here is only $\cdot 12$ mm.

Text-figure 9.



Trichosurus vulpecula. G.L. 7.25 mm. (III. '01).

Horizontal section through the head (S4-4-1), passing through the dorsal region of the optic vesicle (*op.v.*) and through the middle of the left head-cavity (*l.h.c.*). The ventral portion of the proliferating bud on the dorso-lateral wall (*dl.*) and the thickening on the postero-medial wall (*pm.*) are shown, and also the anterior portion (*r.e.*) of the abducens muscle-mass lying posterior to the cavity. Between the latter and abducens muscle-mass runs the oculomotor nerve (III.). $\times 110$ and reduced by $\frac{1}{3}$.

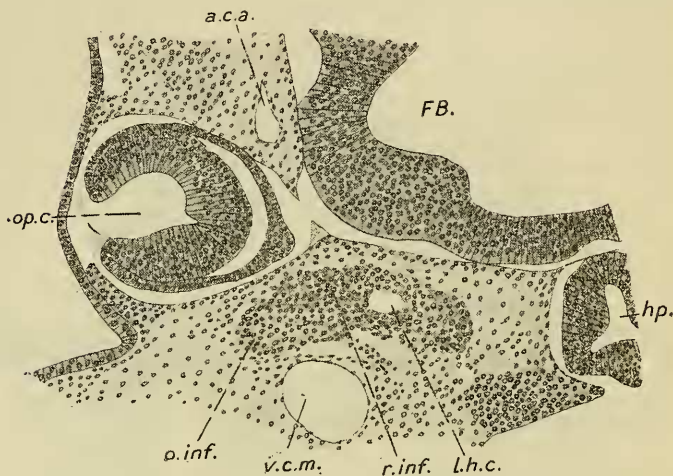
a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *hp.*=hypophysis. *g.V.*=Gas-serian ganglion. *n.c.V.*=Naso-ciliary branch of the trigeminal nerve. *v.c.m.*=vena capitis medialis.

The thickening of the posterior wall is still more marked than in the preceding stage and, joining with the prominent ventral proliferation which now forms a conspicuous outgrowth (text-figs. 10, 12, & 13, *o.inf.*), extends out ventro-laterally to taper off behind and somewhat below the eye. This portion, already

indicated in the 7 mm. and 6 mm. embryos, develops into the future m. obliquus inferior.

On the medial side of the primordium of the m. obliquus inferior at the lower end of the cavity is a darker patch of cells (text-fig. 10, *r.inf.*), the first indication of the m. rectus inferior, which therefore apparently arises from the lateral side of the postero-ventral wall just medial to the m. obliquus inferior.

Text-figure 10.



Trichosurus vulpecula. G.L. 7.25 mm. (III. '01).

Horizontal section through the head (S 5-1-2), passing through the optic cup (*op.c.*) above the optic stalk and through the extreme ventral end of the left cavity (*l.h.c.*) to show the primordium of the m. obliquus inferior (*o.inf.*) and, just medial to the latter, the region from which the m. rectus inferior (*r.inf.*) takes its origin. $\times 110$ and reduced by $\frac{1}{3}$.

a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *hp.*=hypophysis.
v.c.m.=vena capitis medialis.

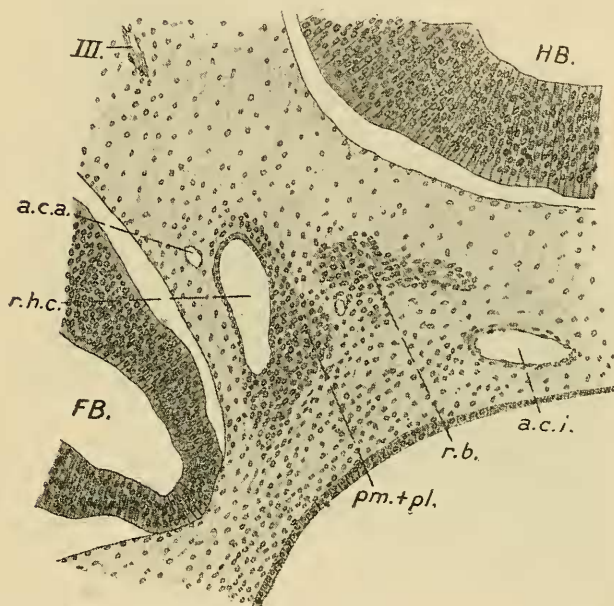
The muscle-bud from the dorso-lateral wall, representing the primordium of the m. rectus superior, is less conspicuous than the other proliferations. It is present on both sides, projecting behind the dorsal part of the optic cup (text-fig. 9, *dl.*); on the right side in (*c*) the bud is less distinct, probably owing to the further thickening of its posterior wall and to the commencing separation of the dorso-lateral portion of the cavity from the rest.

A distinct epithelial layer can only be distinguished on the side next the fore-brain.

The abducens muscle-mass still consists of two portions. The dorsal portion (text-fig. 11, *r.b.*) stretches still further back on the medial side of the vena capitis medialis as a narrow

prolongation into which runs nerve VI and becomes continuous with the anterior part. The latter turns round almost at right angles and runs out laterally immediately behind the postero-lateral wall of the head-cavity (text-figs. 9 & 12, *v.e.*). It tapers ventrally, its lower outer end lying close against the inner portion of the m. obliquus inferior, the two being connected through two or three sections.

Text-figure 11.



Trichosurus vulpecula. G.L. 7.25 mm. (XII A. '02).

Longitudinal section (S9-3-9), passing through the medial side of the right head-cavity (*r.h.c.*) to show the proliferation from the posterior wall (*pm.+pl.*) and the postero-dorsal portion (*r.b.*) of the abducens muscle-mass. $\times 110$ and reduced by $\frac{1}{4}$.

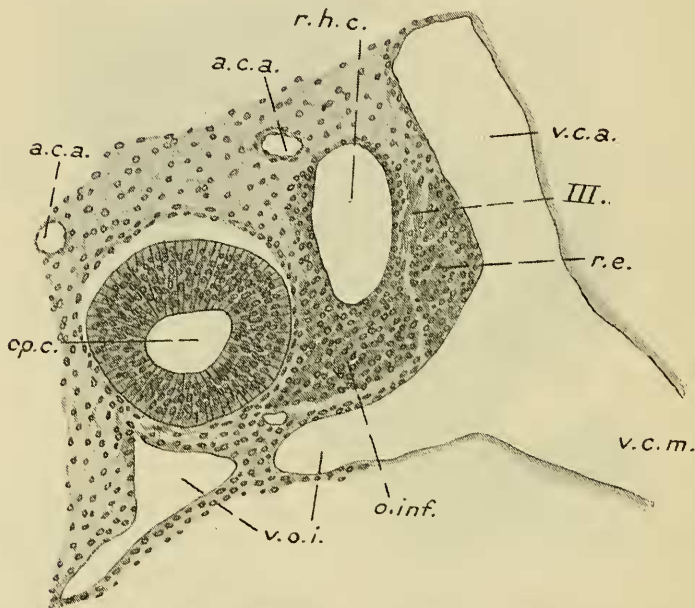
a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *a.c.i.*=arteria carotis interna.
HB.=hind-brain. *III.*=oculomotor nerve.

The trigeminal nerve has now both a supra-orbital and a naso-ciliary branch, running forwards above the bulbus, the naso-ciliary lying on the outer side of the dorsal end of the cavity (text-figs. 9 & 13, *n.c.V.*).

The primordium of the m. obliquus superior is best seen in the longitudinal series (text-fig. 13, *o.s.*). It begins as a collection of cells above and anterior to the optic cup and, extending along the ventral and ventro-lateral sides of the supra-orbital nerve,

it passes backwards and downwards as a solid band of mesenchyme through which runs the naso-ciliary branch of the trigeminal just where this branch joins the ophthalmic. This band continues ventrally, anterior to the Gasserian ganglion, to join the intermediate mass, the latter being connected posteriorly by a thin stream of cells round the antero-ventral side of the same ganglion with the maxillo-mandibular muscle-mass. No union with the maxillo-mandibular mesenchyme can be traced in either

Text-figure 12.



Trichosurus vulpecula. G.L. 7.25 mm. (XII A. '02).

Longitudinal section (S 10-3-1), passing about half-way through the right head-cavity (*r.h.c.*), to show the primordium of the m. obliquus inferior (*o.inf.*) and the anterior portion (*r.e.*) of the abducens muscle-mass lying behind the cavity and immediately in front of the vena capitis medialis (*v.c.m.*) and the vena cerebri anterior (*v.c.a.*). The oculomotor (*III.*) runs down between the cavity and the abducens mass. $\times 110$.

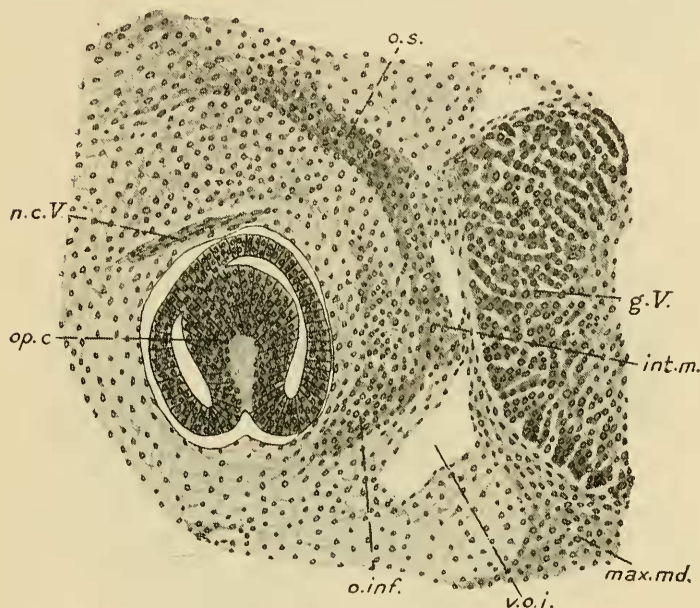
a.c.a. = arteria cerebri anterior. *op.c.* = optic cup. *v.o.i.* = vena orbitalis inferior.

of the transverse series, but the intermediate mass in all three embryos is still joined with the dorsal outer end of the anterior portion of the abducens complex. In the transverse series (*c*) the intermediate mass appears to have lost its connection with the m. obliquus superior and is apparently degenerating.

The oculomotor nerve, descending almost directly ventrally

from the mid-brain, runs close to the postero-lateral wall of the cavity between the latter and the abducens mass (text-figs. 9 & 12, III.). At its distal end it breaks up into many fibres which extend into the postero-lateral proliferation near the point of origin of the m. obliquus inferior.

Text-figure 13.



Trichosurus vulpecula. (XII A. '02.)

Longitudinal section (S 11-1-4), passing through the lateral wall of the cavity and the primordium of the m. obliquus inferior (*o.inf.*). The primordium of the m. obliquus superior (*o.s.*) extends forwards from the intermediate mass (*int.m.*) as a solid band of cells dorsal to the optic cup (*op.c.*). $\times 110$.

g.V. = Gasserian ganglion. *max.md.* = maxillo-mandibular mesenchyme. *n.c.V.* = naso-ciliary branch of the trigeminal nerve. *v.o.i.* = vena orbitalis inferior.

Embryo of G.L. 8.5 mm. ('97 & IV. '01) (=Stage IX. *a* & *b*).
(Text-figs. 14-16.)

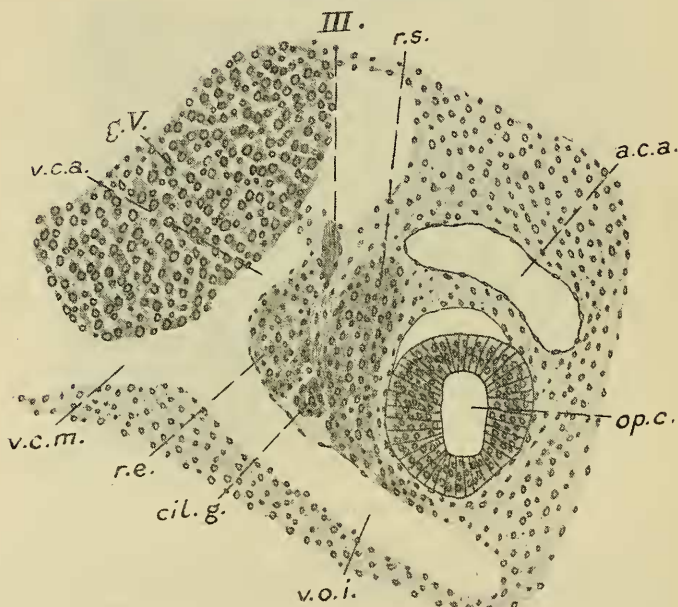
This stage, which measures 8.5 mm. and of which we have two embryos, (*a*) and (*b*), is a good deal more advanced than the preceding one.

The primary optic vesicle still shows a well-marked cavity in the region of attachment of the optic stalk which is still hollow, and pigment is beginning to form in its outer wall. The inner wall of the lens is thickened, its cavity being reduced to a narrow

semicircle, and the eyelid has begun to develop as a fold of the ectoderm on the ventral and posterior sides of the optic cup.

The premandibular cavity is now represented by a mass of mesoderm in which are situated a few cleft-like spaces lying obliquely on each side of the fore-brain (text-fig. 16, *l.h.c.*). On this side the cells have lost almost all traces of their former epithelial character and the spaces are bounded by a thin degenerating layer only a few cells thick; the remaining mesodermal mass, except those parts which are giving rise to the eye muscles, is also breaking down.

Text-figure 14.



Trichosurus vulpecula. G.L. 8.5 mm. ('97).

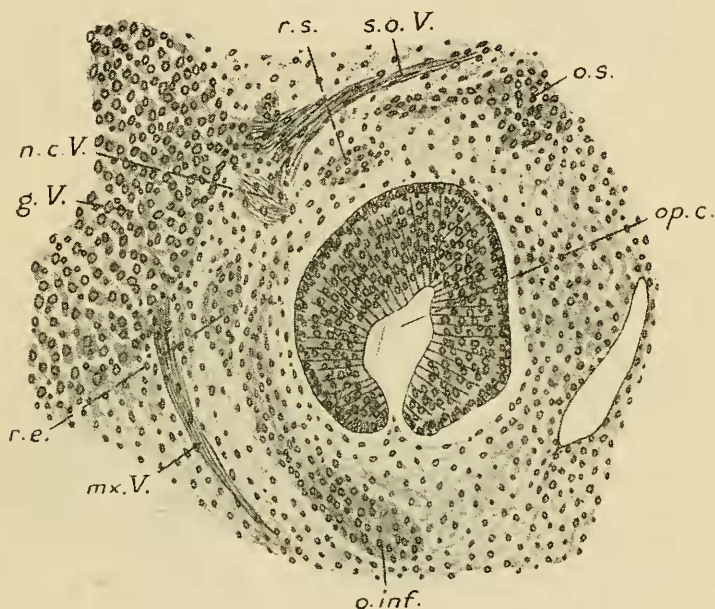
Longitudinal section (S7-1-8), showing the ciliary ganglion (*cil.g.*), the anterior portion (*r.e.*) of the abducens muscle-mass and the primordium of the m. rectus superior (*r.s.*). $\times 110$.

v.a.=arteria cerebri anterior. *g.V.*=Gasserian ganglion. *op.c.*=optic cup.
v.c.a.=vena cerebialis anterior. *v.c.m.*=vena capitis medialis. *v.o.i.*=vena orbitalis inferior. III.=oculomotor nerve.

The dorso-lateral proliferation is now well marked and its cells are undergoing distinct differentiation to form the future m. rectus superior. It has moved dorsally and anteriorly as compared with the last stage, and now lies medial to the dorsal region of the bulbus (text-figs. 14-16, *r.s.*) and is showing signs of becoming independent.

Further ventrally the cavities have completely disappeared and from the now solid mass of cells the m. obliquus inferior runs outwards and downwards behind the eye (text-fig. 15, *o.inf.*). Immediately medial to the m. obliquus inferior the differentiation of cells destined to become the m. rectus inferior extends downwards, its ventral end turning anteriorly, medial to the bulbus and below the optic stalk.

Text-figure 15.

*Trichosurus vulpecula.* G.L. 8.5 mm. ('97).

Longitudinal section (S3-2-8), showing the m. obliquus superior (*o.s.*) with its narrow posterior prolongation and the m. obliquus inferior (*o.inf.*) extending below the optic cup (*op.c.*). The distal end of the m. rectus superior (*r.s.*) and the lateral side of the anterior portion (*r.e.*) of the abducens muscle-mass are also seen. $\times 110$.

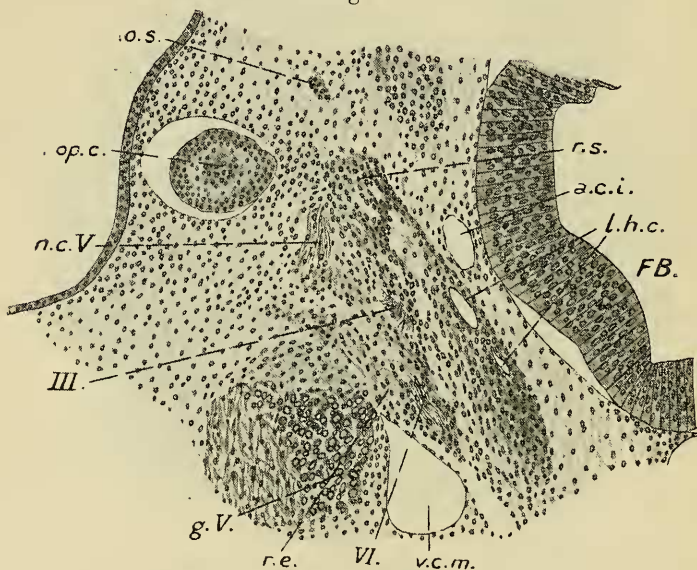
g.V.=Gasserian ganglion. *n.c.V.*=naso-ciliary branch of V. *s.o.V.*=supra-orbital branch of V. *mx.V.*=maxillary branch of V.

The primordium of the m. obliquus superior is now established as an independent structure. Its main portion forms a condensed mass of cells lying anterior and dorsal to the eye, and from this a narrow prolongation projects posteriorly above the bulbus, the higher pointed end of which comes very close to the m. rectus superior (text-fig. 15, *o.s.*). This backward prolongation is obviously the last remnant of the former connection with the intermediate mass (compare Johnson, '13, p. 150). The last

vestiges of the latter can only be recognised in the longitudinal series in front of the Gasserian ganglion and just posterior to the ventral side of the anterior portion of the abducens muscle-mass, with which it is no longer connected; it passes back on the inner side of the root of the maxillary branch of the trigeminal nerve to join with the maxillo-mandibular muscle-mass.

The abducens muscle-mass has not changed in position, except that the posterior dorsal portion does not seem to extend so far backwards, and that the anterior portion has grown out still further laterally (text-figs. 14-16, *r.e.*).

Text-figure 16.



Trichosurus vulpecula. G.L. 8.5 mm. (IV. '01).

Horizontal section through the head (S 7-1-4), showing the last vestiges of the left head-cavity (*l.h.c.*) and the developing m. rectus superior (*r.s.*). The anterior portion (*r.e.*) of the abducens muscle-mass lies in front of the vena capitis medialis (*v.c.m.*) and the Gasserian ganglion (*g.V.*), and in it lies the abducens nerve (VI.). The ventral edge of the m. obliquus superior (*o.s.*) is just seen anterior to the optic cup (*op.c.*). $\times 110$ and reduced by $\frac{1}{4}$.

a.c.i.=arteria cerebri anterior. *FB.*=fore-brain. *n.c.V.*=naso-ciliary branch of the trigeminal nerve. *III.*=oculomotor nerve.

The oculomotor nerve (text-figs. 14 & 16, III.) again divides at its distal end close to the point of origin of both m. obliquus inferior and m. rectus inferior into many fine fibres, some of which penetrate into the m. obliquus inferior itself (see text-fig. 17, III.).

The ciliary ganglion first appears at this stage as a transversely elongated mass of cells, situated between the ventral end of the anterior portion of the abducens complex and the point of origin of the m. obliquus inferior and the m. rectus inferior (text-fig. 14, *cil.g.*).

The trochlear nerve was observed for the first time in the longitudinal series but it could not be made out in the horizontal. It arises in the usual way from the dorsal side of the brain and runs ventrally almost as far as the level of the dorsal border of the Gasserian ganglion.

The first indication of the formation of muscle cells is seen in series (*b*) and is most marked in the mm. recti superior, inferior and externus, less definite in the m. obliquus inferior, and not recognisable at all in the m. obliquus superior.

Embryos of G.L. 9.5 mm. (V. '01) & 10 mm. (VI. '01)
(=Stages X. & XI.). (Pl. I. figs. 1, 2 & text-fig. 17.)

These two embryos, measuring 9.5 and 10 mm. respectively, resemble in many respects those of the last stage but show in some details a slight advance in development.

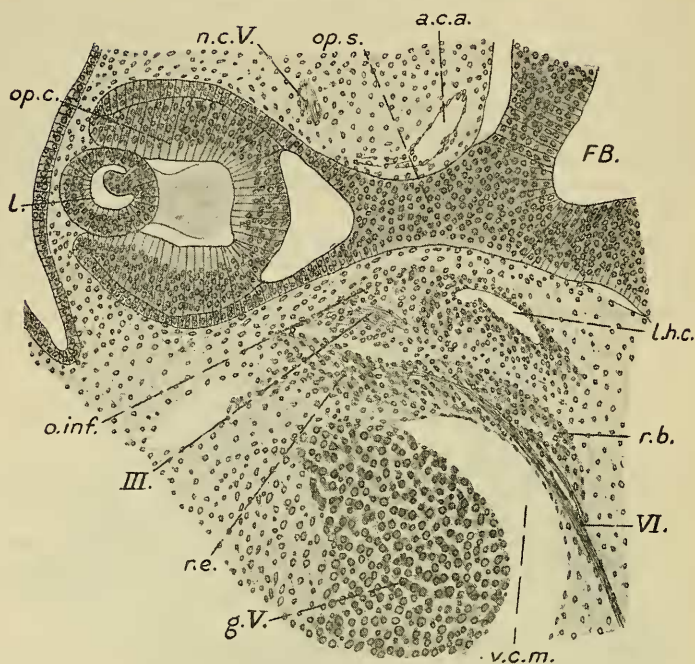
The outline of the eye is more oval and the eyelid has closed over at the extreme ventral side of it. At 10 mm. the cavity of the lens is further reduced and the opening in the optic stalk is narrower.

A slit-like remnant of the head-cavity is still present in both embryos (text-fig. 17, *l.h.c.*). Figs. 1 & 2 (Pl. I.) show posterior and anterior views of a wax-plate model of the embryo of 9.5 mm. The m. rectus superior is now quite conspicuous and has grown forwards and dorsally above the optic cup (figs. 1 & 2, *r.s.*). Below the latter the m. obliquus inferior extends down from the postero-lateral corner of the solid mass of mesoderm which has taken the place of the former head-cavity (fig. 1, *o.inf.*). The m. rectus inferior is now more marked and stretches out anteriorly below the optic stalk (fig. 2, *r.inf.*). The m. obliquus superior (fig. 2, *o.s.*) lies in the same position as in the last stage; but is larger and more prominent and still retains the narrow prolongation running backwards towards the m. rectus superior (fig. 1, *r.s.*). The two portions of the abducens complex are well seen in the model (Pl. I. fig. 1 and text-fig. 17, *r.b.* & *r.e.*) and are very similar to the embryo of 8.5 mm.

At 10 mm. the differentiation of muscle fibres is well established and can be seen in all the developing eye muscles.

In both embryos, at the point of origin of the m. rectus inferior and m. obliquus inferior, a narrow band of mesodermal cells runs directly outwards immediately anterior to the m. obliquus inferior and becomes united with the ventral side of the eyelid posterior to the optic cup (Pl. I. figs. 1 & 2, +).

Text-figure 17.

*Trichosurus vulpecula*. G.L. 9.5 mm. (V. '01).

Horizontal section through the head (S 4-3-5), passing through the optic cup (*op.c.*), optic stalk (*op.s.*) and lens (*l.*), and showing the last vestige of the left head-cavity (*l.h.c.*) and the proximal end of the m. obliquus inferior (*o.inf.*), into which fibres of the oculomotor nerve (III.) penetrate. The two portions (*r.b.* & *r.e.*) of the abducens muscle-mass are well seen and are penetrated by the abducens nerve (VI.). $\times 110$ and reduced by $\frac{1}{4}$.

a.c.a.=arteria cerebri anterior. *FB.*=fore-brain. *g.V.*=Gasserian ganglion. *n.c.V.*=naso-ciliary branch of the trigeminal nerve. *v.c.m.*=vena capitis medialis.

Embryos of G.L. 11 mm., 11.5 mm., & 12 mm. (=Stages XII. & XIII.). (Text-fig. 18.)

The observations were made from six embryos, one of 11 mm. (XII. '04), four of 11.5 mm. (XXII. '04, 5 '97, 9 '98, & VII. '01), and one embryo of 12 mm. (X. '01).

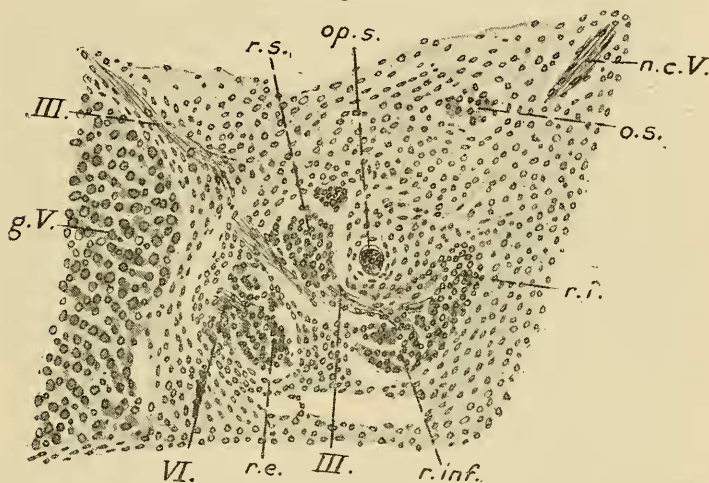
The lumen of the optic stalk is very small and the cavity of the lens is considerably reduced compared with the 10 mm. stage.

A thick strand of cells running postero-medially towards the hypophysis on each side of the fore-brain is all that remains of the unused walls of the former head-cavity. With the lateral end of this strand is connected the m. rectus superior which,

running dorsally outwards, ends above the eye just behind the middle of the latter (text-fig. 18, *r.s.*).

The m. rectus inferior (text-fig. 18, *r.inf.*) arises below the proximal end of the m. rectus superior with which it is joined by a slender connection; it has increased in thickness and passes out ventrally and anteriorly below the optic stalk. Behind the middle region of this muscle, towards its proximal end, a small new offshoot branches out and stretches up dorsally on to the anterior side of the optic stalk; this is the first appearance of the m. rectus internus (text-fig. 18, *r.i.*).

Text-figure 18.



Trichosurus vulpecula. G.L. 11.5 mm. (5'97).

Longitudinal section (S 11-3-5), showing the primordium of the m. rectus internus (*r.i.*) which develops as an outgrowth from the m. rectus inferior (*r.inf.*). The m. rectus externus (*r.e.*), m. rectus superior (*r.s.*), and m. obliquus superior (*o.s.*) are also seen. $\times 110$.

g.V.=Gasserian ganglion. *n.c.V.*=naso-ciliary branch of trigeminal nerve.
op.s.=optic stalk. *III.*=oculomotor nerve. *VI.*=abducens nerve.

The m. obliquus inferior has changed most in position compared with the last stage. It has moved forwards below the bulbus and now runs antero-ventrally outwards, lying some distance in front of the m. obliquus superior above. It is loosely joined to the outer ventral end of the m. rectus inferior, though this connection is nothing more than a few strands in the 11.5 mm. embryo, and its distal end has begun to turn slightly forwards towards the ali-nasal cartilage from which it finally takes its origin.

The m. obliquus superior is now well developed; it has

increased in length and runs from the dorsal anterior side of the bulbus inwards and slightly downwards (text-fig. 18, *o.s.*).

The anterior portion of the abducens muscle-mass (text-fig. 18, *r.e.*), which we may now call the *m. rectus externus*, stretches out laterally in the usual position posterior to the other muscles and just behind the ciliary ganglion, its pointed lateral end extending outwards towards the posterior border of the eye. The inner dorsal portion of the mass, however, is now shorter and its anterior end, which is united with the *m. rectus externus*, has thickened, the thickening being the preliminary stage of the later forward movement of this portion which is the primordium of the *m. retractor bulbi*.

The oculomotor nerve passes ventrally from the mid-brain anterior to the Gasserian ganglion, gives off a twig into the proximal end of the *m. rectus superior*, then goes downwards through the medial side of the ciliary ganglion immediately behind the optic stalk. Leaving the ganglion, it gives off a branch to the *m. rectus inferior* and runs outwards on the postero-lateral side of the latter to send an offshoot to the *m. obliquus inferior* (text-fig. 18, III.). Thus all the oculomotor muscles receive their nerve supply at practically the same time. The ciliary ganglion is slightly larger than at the last stage and forms a transversely elongated mass of cells lying on a level with the optic stalk between the ventral end of the *m. rectus externus* and the proximal end of the *m. rectus inferior*.

The trochlear nerve can now be followed from the dorsal surface of the brain downwards immediately in front of the Gasserian ganglion, its distal end turning forwards to run into the *m. obliquus superior*.

As in the last stage, a strand of mesoderm cells extends laterally from the proximal end of the *m. rectus inferior* to the ventral border of the eyelid, but here, owing to the forward movement of the *m. obliquus inferior* below the bulbus, this strand now lies dorsal and posterior to the latter muscle.

The embryo of 12 mm. only differs in the following respects from the 11.5 mm. The eyelids have folded completely over the eye; all the muscles have increased in size and every trace of the walls of the former head-cavity has disappeared. The attachment of the distal end of the *m. obliquus inferior* to the ali-nasal cartilage has begun and the anterior end of the primordium of the *m. retractor bulbi*, only apparent as a thickening in the last embryo, now projects slightly forwards towards the optic stalk.

Embryos of G.L. 13 & 13.5 mm. (= Stage XIV.).

The stage consists of three embryos, two measuring 13 mm. (*a*) (IX. '01) & (*b*) (XXV.), and the third (*c*) (XXIV.) with a length of 13.5 mm.

The optic stalk is still hollow, though its cavity is very small

and difficult to see in the mid-region of its extent. In (*a*) the eyelids have folded completely over the eye, but in (*b*) they have closed over the lower half only and here the lens is solid. Otherwise the eye resembles that of the last stage.

A vestige of the walls of the former head-cavity is still present in embryo (*a*) only, and is seen as a strand of cells running backwards and inwards from the medial end of the *m. rectus superior*. In (*a*) the latter is an independent muscle, whereas in (*b*) and (*c*) it is apparently still joined with the *m. rectus inferior*.

As the positions of the muscles at this stage are very much the same as at 15 mm., of which a wax model has been constructed, they will be described in detail in the sequel. A few remarks may, however, be made here. The *m. rectus internus* is as yet very short and at 13 mm. the *m. rectus inferior* is still attached to the *m. obliquus inferior*, but the separation of the two muscles is complete at 13.5 mm. The *m. obliquus inferior* is now definitely attached to the ali-nasal cartilage; it has thus changed its position, its outer end turning inwards to the point of attachment, while the proximal end is inserted into the antero-ventral side of the bulbus.

The part of the abducens muscle complex destined to form the *m. retractor bulbi* has grown still further forwards and outwards towards the medial wall of the eyeball. From its lateral side the *m. rectus externus* extends almost directly outwards to the posterior lower wall of the bulbus, the two muscles running out at an acute angle to each other, the *m. retractor bulbi* crossing the inner end of the *m. rectus externus*.

Embryos of G.L. 14, 14.5, & 15 mm. (= Stage XV.).
(Pl. II. figs. 3-5.)

In this stage we have an embryo of 14 mm. (XXIII.), two pouch young of 14.5 mm., *a* (XV. '02) and *b*, and one of 15 mm., the last three being recently born.

The eyelids are now quite folded over but the optic stalk still contains a minute cavity.

The *m. rectus superior* (Pl. II. fig. 4, *r.s.*) runs from behind the inner end of the optic stalk just above the proximal end of the *m. rectus inferior* slightly dorsally and outwards, its pointed outer extremity being inserted in the eyeball dorsal to the posterior side of the latter and at a slightly lower level than the *m. obliquus superior*.

The *m. obliquus superior* (Pl. II. fig. 3, *o.s.*) is now a stronger better developed muscle than at 13 mm. It extends directly outwards over the anterior side of the bulbus, its broad inserted end, which is flattened antero-posteriorly, stretching further laterally over the eyeball than any of the other eye muscles.

The *m. rectus inferior* (Pl. II. figs. 3 & 5, *r.inf.*) arises from below the inner end of the optic stalk and passes downwards and slightly anteriorly below the stalk as a broad muscle which tapers

gradually as it proceeds below the bulbus, its pointed ventral end being inserted close to the *m. obliquus inferior*. Near its wide proximal end, immediately in front of the optic stalk, the *m. rectus internus* branches off and runs outwards with a slightly dorsal trend on to the anterior side of the bulbus close below the *m. obliquus superior* (figs. 3 & 5, *r.i.*). The *m. rectus internus* is as yet a much thinner and shorter muscle than the *m. rectus inferior* but has nevertheless grown considerably since our last stage, now stretching farther laterally and upwards towards its future point of insertion in the eyeball.

The *m. obliquus inferior* (Pl. II. figs. 3-5, *o.inf.*) is no longer connected with the *m. rectus inferior*. It appears as a more or less dorso-ventrally flattened structure of a somewhat oblong shape, having a slightly longer axis in an obliquely antero-posterior direction; as at 13.5 mm., its now proximal but formally distal end is attached to the ali-nasal cartilage, the opposite once proximal end extending towards the lower anterior side of the bulbus.

As regards the abducens complex, we see at 15 mm. very little advance compared with the last stage. The portion corresponding to the *m. retractor bulbi* (figs. 4 & 5, *r.b.*) stretches farther inwards and posteriorly than any of the other muscles; it increases in thickness as it runs antero-laterally and downwards towards the outer end of the optic stalk, its distal end lying just behind the junction of the oculomotor with the ciliary ganglion. In the model this end shows the first indications of growth round the posterior side of the optic stalk, but this growth round the stalk is, however, more marked in 14 mm. and 14.5 mm. The *m. rectus externus* (figs. 4 & 5, *r.e.*) stretches from the lateral side of the *m. retractor bulbi*, not far from the anterior end of the latter, outwards and downwards, its outer pointed end lying below the postero-ventral side of the bulbus some distance behind the outer end of the *m. obliquus inferior*.

The abducens nerve extends forwards from its origin and then downwards on the outer side of the *m. retractor bulbi*, running into the abducens complex at the region where the two components of the latter are joined with one another (fig. 4, VI.).

The oculomotor nerve (Pl. II. figs. 3-5, III.) runs forwards medial to the naso-ciliary branch of the trigeminal into the posterior end of the *m. rectus superior*, and continues obliquely outwards and downwards close against the inner end of the ciliary ganglion and along the side of the *m. rectus inferior* next the eye. It gives off fibres on this same side into the root of the *m. rectus internus*. Leaving the *m. rectus inferior* before the latter reaches the bulbus, it passes anteriorly and ventrally into the *m. obliquus inferior*.

The ciliary ganglion forms an elongated mass of cells stretching out below the optic stalk; at 15 mm., as seen in the model (fig. 5, *cil.g.*), it is not so elongated as in some of the examples measuring 13 mm. and 14 mm.

The distal end of the trochlear nerve (figs. 3-5, IV.) runs forwards and outwards into the posterior side of the medial end of the m. obliquus superior.

The naso-ciliary branch of the trigeminal nerve (figs. 3-5, V.) passes out immediately lateral to the oculomotor, downwards below the posterior side of the m. rectus superior, and forwards above the optic stalk and along the anterior lower border of the medial end of the m. obliquus superior to the snout.

Fœtus of G.L. 17 and of 17.5 mm.

This stage consists of two pouch young, one measuring 17 mm. and the other 17.5 mm. The optic stalk has quite disappeared and the eye muscles have practically attained their adult positions.

The distal end of the m. obliquus superior turns posteriorly and comes to lie so close to the outer end of the m. rectus superior that the two muscles are inserted almost at the same place.

The m. rectus internus has increased greatly in size and is now a well-developed muscle; it is, however, still connected with the m. rectus inferior at its proximal end by a thin band of cells.

The m. obliquus inferior, as in our last stage, runs obliquely backwards from the ali-nasal cartilage, its posterior end now being inserted anterior to and on the lateral side of the m. rectus externus.

The m. rectus externus and the m. retractor bulbi are now separate muscles. The former is inserted on the posterior side of the bulbus; at about its mid-region on the anterior side, an indentation is present which in all probability represents the first indication of the later division of the muscle into two portions. The m. retractor bulbi has developed considerably; it extends from the middle of the basisphenoid cartilage, to which it is becoming attached, anteriorly and outwards, its distal end surrounding the posterior side of the optic nerve in the shape of a half moon, the pointed ends of which stretch out, the one above, the other below the nerve. The m. retractor bulbi is innervated by a small branch from the abducens nerve before the latter runs into the m. rectus externus.

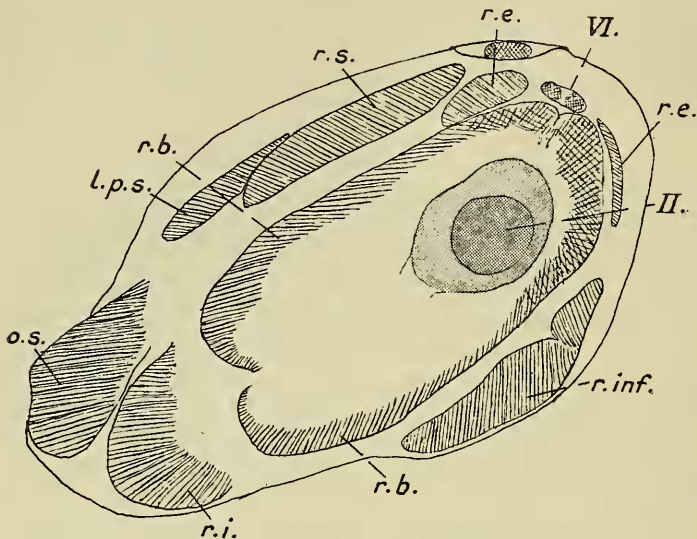
Fœtus of G.L. 5.2 cm. (Text-fig. 19.)

The m. retractor bulbi (text-fig. 19, *r.b.*) has now attained its adult position. It enters the orbit on the posterior side of the optic nerve and, surrounding the latter, stretches outwards as a circular sheet of muscle gradually diminishing in thickness and increasing in circumference up to its insertion round the inner side of the bulbus within the recti muscles. The two edges of the sheet lie close together, especially at its outer end, but they never completely fuse.

The proximal end of the m. rectus externus (text-fig. 19, *r.e.*) is split up into two portions, already indicated at 17 mm., which

unite distally to have a single insertion on the posterior side of the bulbus.

Text-figure 19.



Trichosurus vulpecula. G.L. 5.2 cm.

Longitudinal section (S23-1-5) passing through the optic nerve (II.) and the surrounding eye muscles. The m. retractor bulbi (*r.b.*) forms a circular sheet of muscle within the other eye muscles. The two portions of the m. rectus externus (*r.e.*) are also seen. $\times 35$.

l.p.s.=levator palpebrae superioris. *o.s.*=m. obliquus superior. VI.=abducens nerve. *r.i.*=m. rectus internus. *r.inf.*=m. rectus inferior. *r.s.*=m. rectus superior.

Summary of Events in Trichosurus vulpecula.

In early stages a large premandibular cavity surrounded by a single epithelial layer of cells is present on each side of the fore-brain posterior to the optic vesicles.

In the 7 mm. embryo an extensive thickening occurs on the lower two-thirds of the posterior wall, later (in the 6 mm. embryo) extending on to the ventral wall of the cavity. From this thickening the m. obliquus inferior and the common primordium of the m. rectus inferior and m. rectus internus develop, the first to appear being the m. obliquus inferior which grows out laterally as a solid protuberance from the ventro-lateral side; the m. rectus inferior arises a little later (in the embryo of 8.5 mm.) as a forward extension from the thickened wall immediately medial and slightly ventral to the m. obliquus inferior.

As development proceeds, the *m. obliquus inferior* moves forwards below the eye, its distal end turning inwards in the 11.5 mm. embryo to become attached to the ali-nasal cartilage. It becomes independent in the 13.5 mm. embryo and its originally proximal end moves outwards to reach its final insertion on the antero-ventral side of the bulbus. This muscle thus undergoes a noteworthy change in position. The *m. rectus inferior* grows forwards and outwards, becomes independent and finally extends downwards from below the inner end of the optic cup to become inserted in the ventral side of the bulbus close to the *m. obliquus inferior*.

From the dorso-lateral region of the cavity in the 6 mm. embryo appears a bud-like outgrowth whose surrounding walls, especially that of the posterior side, proliferate and give rise to the *m. rectus superior*. The primordium of this muscle grows antero-posteriorly over the eyeball, becomes independent and very early attains its final position (11 to 12 mm.).

The remaining walls of the head-cavity undergo degeneration and become obliterated in the surrounding mesenchyme.

The *m. rectus internus* is the last of the eye muscles to make its appearance. It first develops in the 11 mm. embryo as an outgrowth from near the proximal end of the *m. rectus inferior* and grows dorso-laterally to become inserted on the anterior side of the bulbus.

The abducens complex is first seen as a solid mass of cells lying posterior to the premandibular cavity and consisting of postero-dorsal and antero-ventral portions. The latter grows out laterally as the *m. rectus externus* and the former grows forwards and outwards, crossing the inner end of the *m. rectus externus*, its distal end finally surrounding the optic nerve as the *m. retractor bulbi*. The *m. retractor bulbi* is the last of the eye-muscles to assume its final position.

The *m. obliquus superior* takes its origin from a mass of cells, termed by me the intermediate mass, which can be traced downwards into continuity with the maxillo-mandibular mass of mesenchyme. The anterior band-like part of the intermediate mass separates off to form the primordium of the *m. obliquus superior*. It grows inwards to form a muscular band, which extends out from above the *m. rectus internus* to the anterior side of the bulbus.

The more posterior portion of the intermediate mass, attached to the maxillo-mandibular mesenchyme, is wider and composed of more loosely arranged cells, and is also connected in our earlier stages with the lateral side of the primordium of the *m. rectus externus* and for a still shorter period with the postero-lateral wall of the head-cavity. After the *m. rectus externus* and the *m. obliquus superior* become independent the intermediate mass disappears.